

THE ARMoured DINOSAUR *POLACANTHUS FOXI* FROM THE LOWER CRETACEOUS OF THE ISLE OF WIGHT

by WILLIAM T. BLOWS

ABSTRACT. A new specimen of the Lower Cretaceous nodosaurid ankylosaur *Polacanthus foxi* was found in the Wealden formation of the Isle of Wight in 1979. Three types of presacral spine are now recognized and new dermal elements of unknown position were found. Cranial and cervical fragments are described for the first time, including an axis formerly identified by Seeley, 1876, as *Iguanodon*. The sacrum shows a widening of the neural canal, as in *Stegosaurus* and others, and the tail plates differ from those of the holotype. The systematic status of *P. foxi* is reviewed, and comparisons are made with other contemporary nodosaurid taxa as far as possible. The genus *Polacanthus* appears to be valid despite suggested synonymy with *Hylaeosaurus*, it may, however, have closer affinities with contemporary taxa of the New World, notably *Hoplitosaurus*. *Polacanthus* appears to have a greater geological range than *Hylaeosaurus*.

LEE (1843) described and illustrated three pieces of saurian dermal plates which, at the time, were unknown to science. These specimens can now be identified as fragments of sacral dermal plate of *Polacanthus*. The site of these pieces is recorded as the 'Hastings Sands' of Sandown Bay, Isle of Wight. According to Rawson *et al.* (1978) the Hastings Beds do not outcrop on the Isle of Wight, and the specimens probably came from the Wealden Marls (Wessex Formation), the usual horizon for *Polacanthus*. Not only is this possibly one of the earliest descriptions of *Polacanthus* material (without using the name), but Lee's manuscript has a footnote telling of the loss of these specimens in a hackney coach.

In 1865 William Fox excavated a partial skeleton of an armoured dinosaur from Barnes High, near Atherfield, Isle of Wight (Blows 1983). Much of the pelvis, hind limbs, and vertebral column were collected together with considerable dermal armour, which was made the type of *P. foxi*. A journal (Anon. 1865) described this discovery in a brief notice accompanied by a drawing of a collection of these bones. This account also included the name *Polacanthus* for the first time, and attributed this name to Owen. Huxley (1867) mentioned the name during an account of *Acanthopholis*, and again attributed it to Owen. However, Huxley is the earliest known author of the name. Hulke (1881, 1887) made a full description of the remains when they arrived in London in 1881. Again he attributed the name to Owen.

Since this time, only one other important specimen of *Polacanthus* has been described (Lydekker 1891) also from the Isle of Wight. It is a portion of the pelvis with some overlying dermal armour. This armour was thought to be smooth rather than patterned (as in *P. foxi*) and this led to the suggestion that it could be a new species (Seeley 1891), later called *P. becklesi* Hennig 1924, after the collector Mr Beckles. However, this species is here synonymized with *P. foxi*. Other genera of contemporary age are *Hylaeosaurus* Mantell 1833, *Polacanthoides* Nopcsa 1928, and *Hoplitosaurus* Lucas 1902, all based on inadequate material, and their affinities with *Polacanthus* are poorly understood.

The object of this paper is to describe the most recent discovery of *Polacanthus* (Blows 1982) which was collected by the author from Compton Bay beach, Isle of Wight from 1979 to 1984.

Abbreviations. AMNH, American Museum of Natural History; BMNH, British Museum (Natural History); BYU, Brigham Young University; GM, Gosport Museum; KU, Kansas University; MIWG, Museum of Isle

of Wight, Geology; CAMSM, Sedgwick Museum Cambridge; USNM, United States National Museum; YPM, Yale Peabody Museum.

SYSTEMATIC PALAEOLOGY

Order ORNITHISCHIA

Suborder ANKYLOSAURIA

Family NODOSAURIDAE

Genus *Polacanthus* Huxley 1867

Type species. *P. foxi* Hulke 1881.

Holotype. BMNH R175, partial skeleton with dermal armour (Fox Collection).

Type locality. Barnes High, West of Cowleaze Chine, Atherfield, Isle of Wight (NGR SZ 443 806).

Type horizon. Wealden Marls (Wessex Formation), Lower Cretaceous (Barremian).

Range. Wealden Marls (Wessex Formation) to Ferruginous Sands (?) (Aptian).

Diagnosis. Moderate to large size nodosaurid (Coombs 1978); presacral series of five fused vertebrae; sacrum of five fused vertebrae; maximum sacral canal expansion at S2 level; five sacral ribs; long posterior dorsal ribs supporting overlying dermal armour and adjoining anterior ilium; ribs flat dorsally, supported by a ventral ridge giving a T-shaped cross-section; anterior caudal vertebrae with long lateral processes, thickened neural process with a supraspinous notch; caudal series terminating in a vertebral-dermal mass with ossified tendons (?primitive club); presacral dorsal spines attain maximum heights over the shoulder region, reducing in height both anteriorly and posteriorly; the spines have flattened bases, the dorsal keel in large specimens twist through nearly 90° from base to apex, presacral spines mounted in a double row laterally to the spinal column; presacral 'lumbar', sacrum, and both ilia covered by a large, flat dermal plate of armour, approximately 1 m square, ornamented on the dorsal surface by ossifications; caudal armour of tall upright or short roof-like plates in double row, descending in height posteriorly and having narrow, hollow bases; rounded, oval, or subtriangular ossicles of sizes up to 110 mm across.

Referred specimens. BMNH R9293, three skull fragments (?nasal, supraoccipital, angular); left neural arch of atlas; CAMSM B53371, axis vertebra; BMNH R9293, (?)fourth cervical vertebra, four dorsal vertebrae and vertebral processes; sacrum with part neural arch; two caudal vertebrae (?first and second); two fragments of ilium; ?portion of ischium; two ribs complete; parts of three more ribs; rib head and fragments; terminal phalanx; ossified tendons; numerous endoskeletal fragments; five dermal plates (caudal series); four dermal spines (presacral series), two dermal spines (presacral series), one spiked plate (?caudal); ten large pieces of sacroiliac shield; fifteen smaller pieces of sacro-iliac shield; thirty-six dermal ossicles; CAMSM B53353, dermal ossicle; CAMSM B53354-53358, five dermal ossicles; CAMSM B53588-53591, four ossicles; CAMSM B53594-53597, four dermal ossicles; BMNH R9293, numerous dermal fragments; small complete bone (one side of bilateral pair) of unknown origin; CAMSM B53372, small complete bone (the other side of bilateral pair) of unknown origin.

Locality. The remains lay scattered within a confined pocket exposed at very low tide on Compton Beach, Isle of Wight (NGR SZ 374 845).

Horizon. The site occurs in the lowest beds of the Wealden Shales (Vectis Formation) and represents the first recorded find of *Polacanthus* from this stratigraphic unit (Dr A. Insole, pers. comm.). The bed is a pale grey, non-fissile, massive clay generally devoid of fossils. The strata dip strongly to the west and can be traced in the corresponding cliff section.

DESCRIPTIVE ANATOMY

The skeleton was disarticulated with bones at different depths. They may have been eroding out for some time. The axis vertebra (described Seeley 1876) and fourteen pieces of dermal armour were

registered at Cambridge Sedgwick Museum between 1860 and the 1940s, and are considered to be the same skeleton as R9293. The (?)fourth cervical vertebra was registered with the British Museum (Natural History) (R9293) in the 1960s, and the main pocket of bones was found and excavated by the author from 1979 to 1984. Other elements may have washed out over this time span to be destroyed by sea action, or be held by private collectors.

The area containing the remains was about 4 square metres. The lack of duplicated bones, beyond that found within one skeleton, plus the rarity of nodosaurid finds in the Weald, suggests the presence of a single animal. Large bones were smashed (e.g. pelvis and overlying armour), and scattered with some loss.

Skull. The holotype of *Polacanthus* is without a skull. A referred specimen, a basisphenoid (BMNH R4951) from the Isle of Wight, is suggestive of nodosaurids but cannot be assigned to a genus with any certainty. A 'lower jaw' (BMNH R175X) has been identified as a fragment of an *Iguanodon* ilium (D. Norman, pers. comm. 1976). The new skeleton has two skull fragments and one possible jaw fragment.

Nasal. This is a flat bone with only one edge and one corner intact. One surface is rounded with grooves, the other is gently depressed with flat dermal ossifications. The preserved edge appears to be part of the medial suture across the skull roof.

Supraoccipital. This is a fragment of bone found loose on the site. It is massive compared to *Stegosaurus* and *Silvisaurus*, with a deeply roughened sutural surface for articulation with the paraoccipital bone, and a smoother articulation surface for the parietal bone. The ventral surface is grooved, the roof of the brain case, and together with the opposite smooth dorsoposterior surface, wedges towards the foramen magnum.

Lower jaw. The jaw fragment is probably the left angular (Galton, pers. comm. 1983). It is a boat-shaped bone with a deeply concave inner surface, and a convex outer surface bearing a dermal ossification. One edge is smooth and sharp, the other is irregular and gently curved.

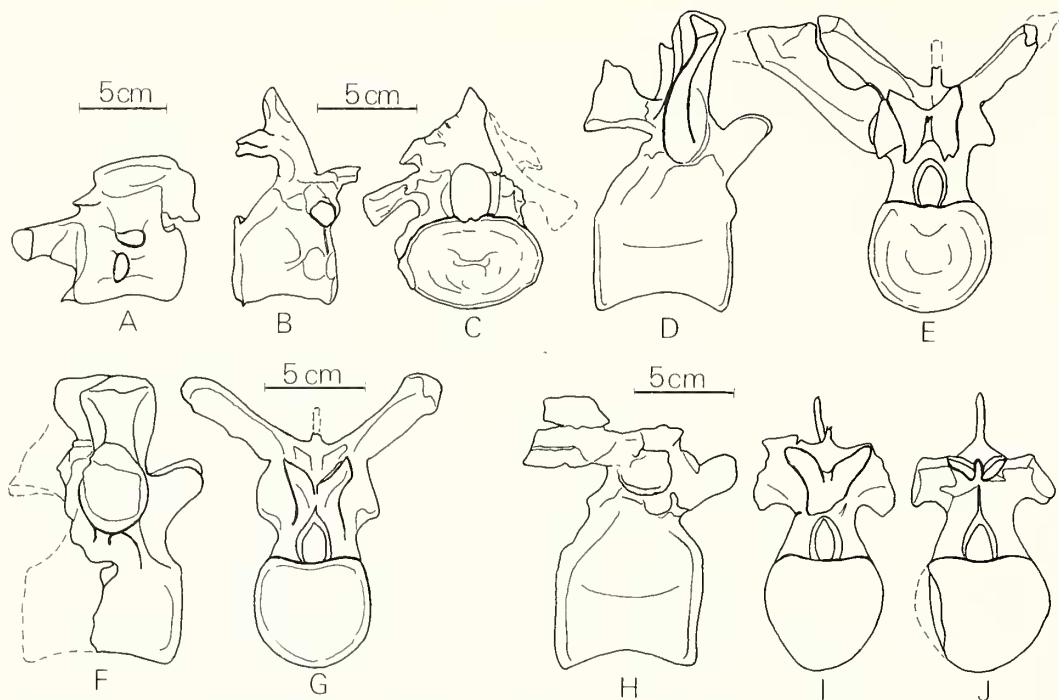
The dentition of *Polacanthus* is unknown.

Post-cranial skeleton

Cervical vertebrae. The entire cervical series is missing in the holotype. A single cervical vertebra, considered as part of the type (BMNH R175) is referable to an ornithopod, probably *Iguanodon*. In the new specimen, one cervical element (from the atlas vertebra) is known from the site. However, an axis vertebra (SMES B53371) and a (?)fourth cervical (BMNH R9293) are from the same locality and probably from the same skeleton (test-fig. 1). The atlas as preserved, consists of only the left neural arch. The right neural arch and intercentrum are missing. The atlas and axis vertebrae were not fused in *Polacanthus*. The atlas corresponds well with *Stegosaurus* as described by Gilmore (1914) except the narrowing below the processes, being more constricted anteriorly and overlain by a pronounced prezygapophysis. The neural arch was not fused to either the intercentrum or the neural arch of the other side along the mid-line, which corresponds with a sub-adult status. The posterior process is missing.

The axis vertebra. Seeley (1876) first described this bone (CAMSM B53371) and regarded it as 'probably *Iguanodon*'. The characteristics are those of general ornithischian dinosaurs and are well described by Seeley (text-fig. 1A). The presence of both diapophysis and parapophysis indicate the double-headed nature of the cervical rib.

(?)Fourth cervical vertebra. Parts of the neural process, the left pre- and postzygapophysis and left lateral process only are missing in this specimen (BMNH R9293) (text-fig. 1B, C). The centrum is amphiplatyan, the articular surfaces being nearly a third greater in width than height and centrally depressed. The large neural canal is ovoid, being greater in height than width. The floor of the neural canal dips downwards to create a central cavity within the centrum. The

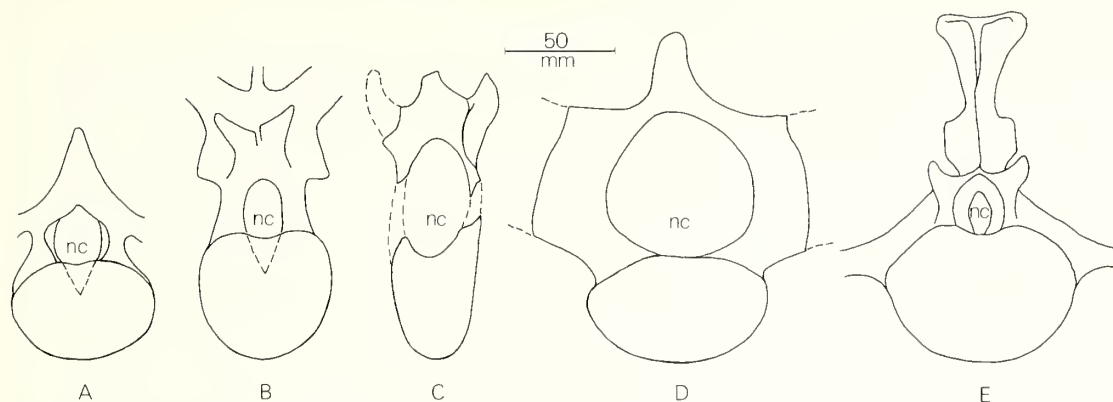


TEXT-FIG. 1. *Polacanthus foxi*. Lower Cretaceous, Isle of Wight. A, SMES B53371, axis vertebra, left lateral view. B, C, BMNH R9293, (?)fourth cervical vertebra. B, right lateral view; C, anterior view. D, E, BMNH R9293, dorsal vertebra. D, right lateral view; E, anterior view. F, G, BMNH R9293, dorsal vertebra. F, right lateral view; G, anterior view. H-J, BMNH R9293, dorsal vertebra. H, right lateral view; I, anterior view; J, posterior view.

pre- and post-zygapophyseal articular surfaces lay approximately on the same horizontal level, the prezygapophysis only extending beyond the limits of the centrum. The neural process is inclined posteriorly.

Dorsal vertebrae. Four free dorsal vertebrae exist in both the holotype and the new specimen. These latter are better preserved than the type, but in both, the vertebrae consist of two almost complete (R175 numbered C12, C14 and R9293 numbered 3, 4); one with only half a centrum (R175 numbered C16, R9293 numbered 2); one being a centrum only (R175 numbered C19, R9293 numbered 1). Other isolated dorsal vertebrae (BMNH 2527; MIWG 5188; CAMSM B53587) are worthy of description. Hulke (1881) and Nopcsa (1905) described the main features of the dorsal vertebrae, but in the new specimen the floor of the neural canal dips into the centrum in a V-shaped manner, with a maximum depth half-way along the vertebral length, similar to the cervicals previously described (text-fig. 2A, B). It occurs in all four vertebrae but is obscured by matrix in the holotype, although fractures across the centra indicate this feature.

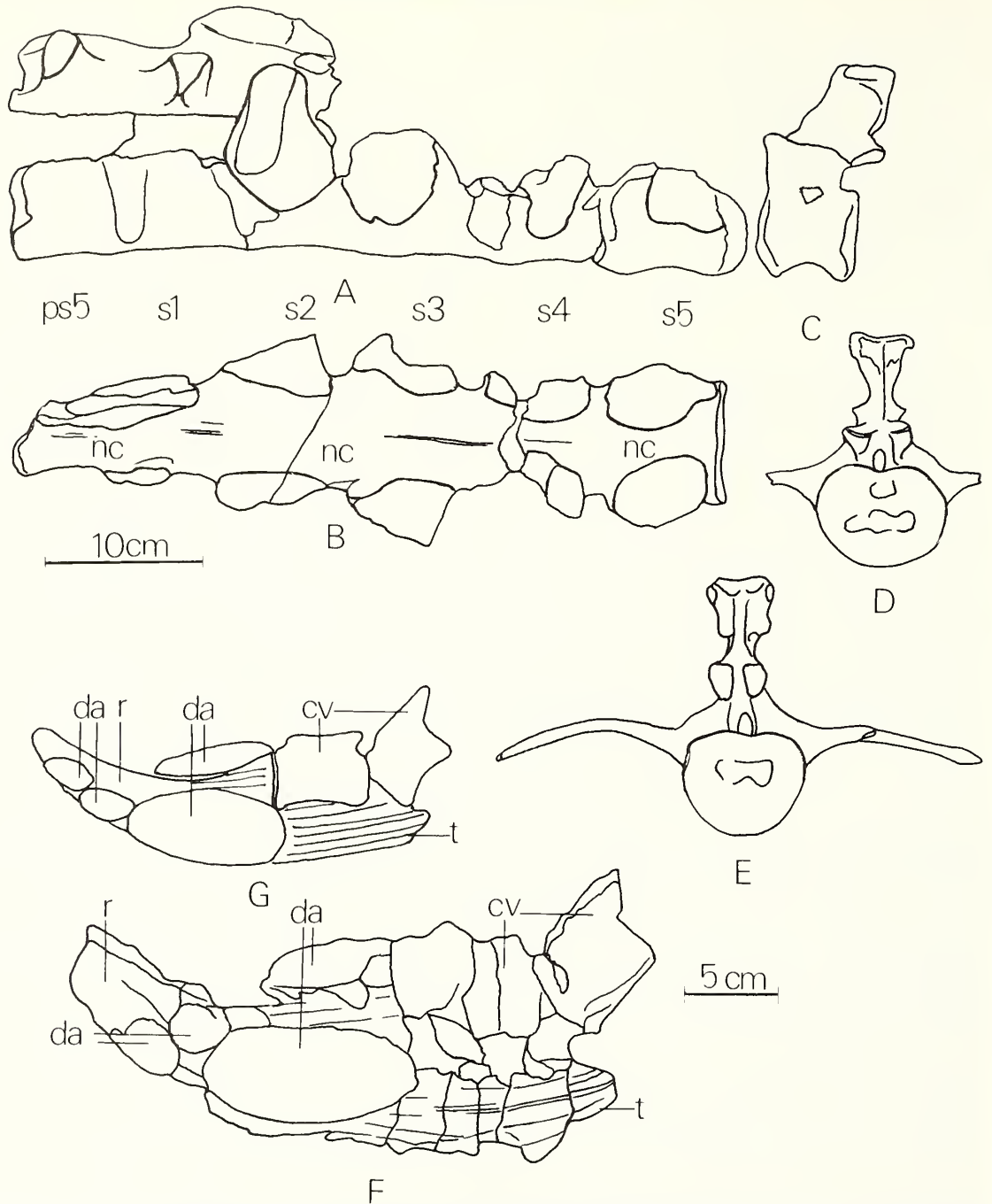
An isolated dorsal vertebra (BMNH 2527) from Barnes High, Isle of Wight (Hulke Collection) is much larger than the other *Polacanthus* Vertebrae (see table of measurements). Another dorsal vertebra from Atherfield, Isle of Wight (SMES B53587), is almost complete. It has transverse processes angled at 60° rather than the usual 90° . A dorsal centrum (MIWG 5188) is complete and unworn. Sutural grooves on each side of the neural canal suggests a juvenile nature. The neural canal floor dips as previously described although partly filled with matrix.



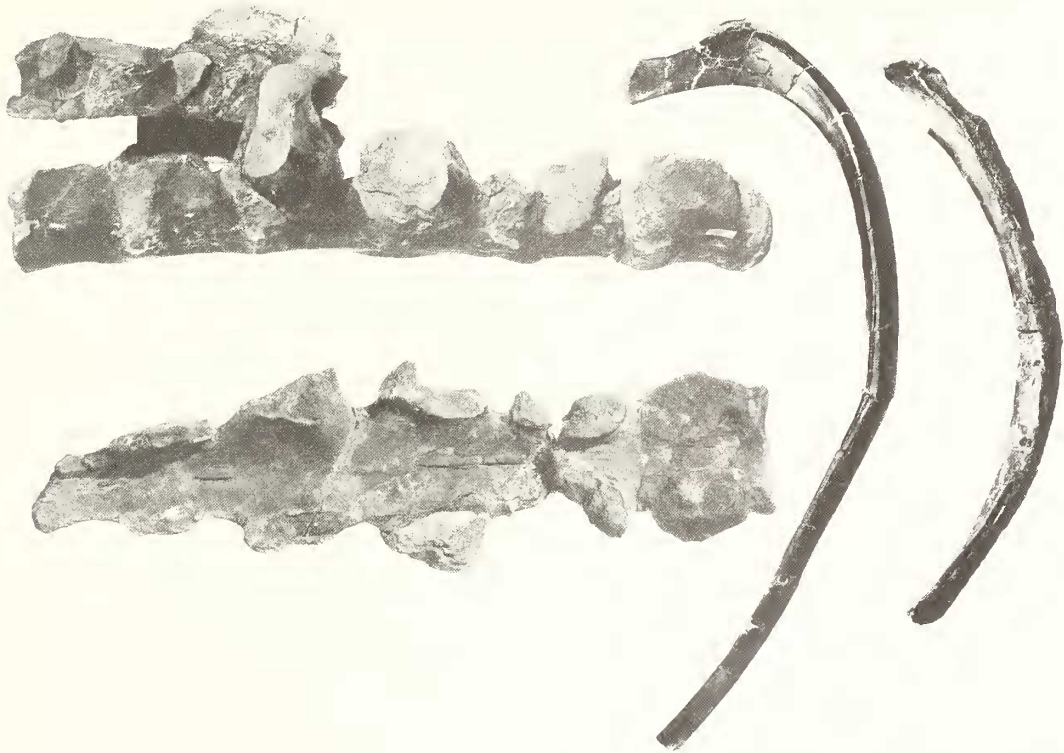
TEXT-FIG. 2. *Polacanthus foxi*. Lower Cretaceous, Isle of Wight. A-E, BMNH R9293, vertebrae showing neural canal (nc). A, cervical vertebra; B, dorsal vertebra; C, anterior sacral vertebra; D, sacral vertebra at S2 level; E, caudal vertebra.

Sacrum. The sacrum (text-fig. 3A, B) is well understood from the holotype which has five vertebrae, with a further five presacral ('lumbar') vertebrae fused into a presacral rod. The holotype has part of the overlying dermal plate and ossified tendons attached. The new specimen of five sacral centra and one presacral centrum is free from attachments, and the neural canal is fully exposed. Nopsca (1905) stated 'There does not seem to exist any especial widening out of the neural canal in the sacral region, as recorded for *Stegoceras* (*sic*- *Stegosaurus*) and also visible in *Dacentrurus* (*Omosaurus*)'. However, sacral neural canal expansions are reported in other nodosaurids: *Sauropelta* (Ostrom 1970), *Nodosaurus* (Lull 1921), *Panoplosaurus* (Sternberg 1921), and *Silvisaurus* (Eaton 1960), and some ankylosaurids (Maryanska 1977). In BMNH R9293 an extensive broadening of the canal reaches a maximum width and height at the level of the second and third sacral vertebrae, confirming this feature in *Polacanthus*. In this respect *Polacanthus* resembles *Stegosaurus*, where a neural expansion occurs over the anterior half of the sacral canal (Gilmore 1914). The holotype sacrum bears five pairs of sacral ribs, the first pair are least robust, arising between the centre of the posterior presacral and first sacral vertebrae. The following three pairs are the most stout, and the posterior ribs arise from the centrum of sacral 5. The sacral ribs and posterior neural arch of the new specimen are missing. A third sacrum from the beach near Whale Chine, Isle of Wight, in a block of sandstone (BMNH no number) bears all the sacral ribs which unite distally prior to the iliosacral joints, as in the holotype. The ventral surface only is exposed, the first two anterior presacrals are missing and two sacral centra are eroded. This is the first recorded discovery of *Polacanthus* in the (?) Ferruginous Sands (F. A. Middlemiss, pers. comm.).

Caudal vertebrae. Nopsca (1905) noted a discrepancy in the holotype tail vertebral count; there are in fact twenty-one preserved. A tail-end mass consisting of two vertebrae, dermal armour, and ossified tendons are included in this number (text-fig. 3F-G). Also the first caudal vertebra is attached to the posterior sacrum at an angle by matrix and may have been regarded as sacrum, or sacrocaudal, and remained uncounted. Both Hulke (1881) and Nopsca (1905) missed this vertebra in their text, regarding the first free vertebra as caudal 1, although Hulke (1887) figures and labels this vertebra (c.v., caudal vertebra). The tail-end mass has a rod-like bone tapering to almost a point representing the termination of the vertebral column. This curves dorsally towards the tip and is hidden mostly by overlying dermal ossifications. It must be a fusion of terminal vertebrae. Two larger dermal plates attached to the mass represent the termination of a tail long bilateral row of plates. Only one surface of the right plate is exposed, the left plate shows two surfaces with a sharp keel-edge. Irregular dermal ossicles are scattered over the vertebral rod between and beyond the plates up to the tail



TEXT-FIG. 3. *Polacanthus foxi*. Lower Cretaceous, Isle of Wight. A-E, BMNH R9293, vertebrae. A, sacrum and anterior neural arch in left lateral view, ps—presacral, s—sacral vertebrae; B, sacrum in superior view showing neural canal (nc); C, first caudal vertebra, left lateral view; D, first caudal vertebra, anterior view; E, second caudal vertebra, posterior view. F-G, BMNH R175, caudal end mass. F, right lateral view, cv—caudal vertebra, da—dermal armour, r—rod of bone, t—tendons; G, restored caudal end mass, right lateral view (see F for abbreviations).



TEXT-FIG. 4. *Polacanthus foxi* Lower Cretaceous, Isle of Wight. BMNH R9293 sacrum and ribs. *Left*: Sacrum, lateral and superior views. *Right*: Ribs.

tip. A group of tendons run throughout the length of the mass along the ventral surface to end at the tail tip. The two caudals found with R9293 are most likely to be the first and second. The second caudal has lateral processes which are thin and long, and both have stegosaur-like expansions of the neural process with a supraspinous notch. A small proximal vertebra (BMNH R4952) from Grange Chine, Isle of Wight, may be the first caudal of a junior individual. A caudal vertebra (MIWG 5144) from Brook Bay, Isle of Wight, is a heavily pyritized, water worn centrum.

Ribs. The holotype has ten free anterior dorsal ribs (labelled left: L4, 5, 7, 8, 9, 10; and right: R3, 6; with two unlabelled) and ten posterior dorsal ribs, five each side attached to the overlying sacral armour. The new specimen has one complete anterior dorsal rib (text-fig. 4), fragments of three others, a rib head attached to a dorsal vertebra, one almost complete posterior rib with evidence of sacral shield attachment, and a few rib fragments. Hulke (1881) describes the ribs sufficiently to establish their major features, including those of the type that are found on the ventral sacral shield (Hulke 1887). These arise from the presacral 'lumbar' vertebrae, although their attachment to the vertebrae is now missing in the holotype. The broad dorsal surfaces of these ribs, in contact with the sacral shield above, are supported by a narrow ventral ridge throughout much of their length. The most anterior of these ribs are the longest, extending flat, bilaterally to beyond the medial edge of the ilia, the posterior three appear to fuse with the ilia. A similar situation, without the sacral shield, occurs in *Euoplocephalus* (Coombs 1978, text-fig. 13). These ribs would not have needed to curve very much proximally in order to unite with the presacral vertebrae in the holotype. However, ribs of a similar nature (new specimen R9293 and R4134) show considerable curvature, suggesting that the vertebral column was deeper set than the holotype shows. This is further supported by the

steep angle of the lateral process on the sacral neural arch of the new specimen. Nopcsa (1905) draws attention to evidence that shows a space existed between the ribs and sacral shield. There is evidence that suggest the pelvic region at least, in the holotype, has been crushed (see pelvis below).

It is possible that the dorsal ribs anterior to the sacro-lumbar unit was deep set below the maximum height curvature of the ribs, and this is supported by the steep angles of the vertebral lateral processes found in dorsal vertebrae (Nopcsa 1905). This feature is seen in *Palaeoscincus* (Gilmore 1930, fig. 11) where the neural process hardly reaches the maximum rib height. Presacral ribs differ from anterior dorsal ribs by a strong 'T' cross-section, the dorsal platform roughened by fibrous tissue compared to the smooth ventral surfaces.

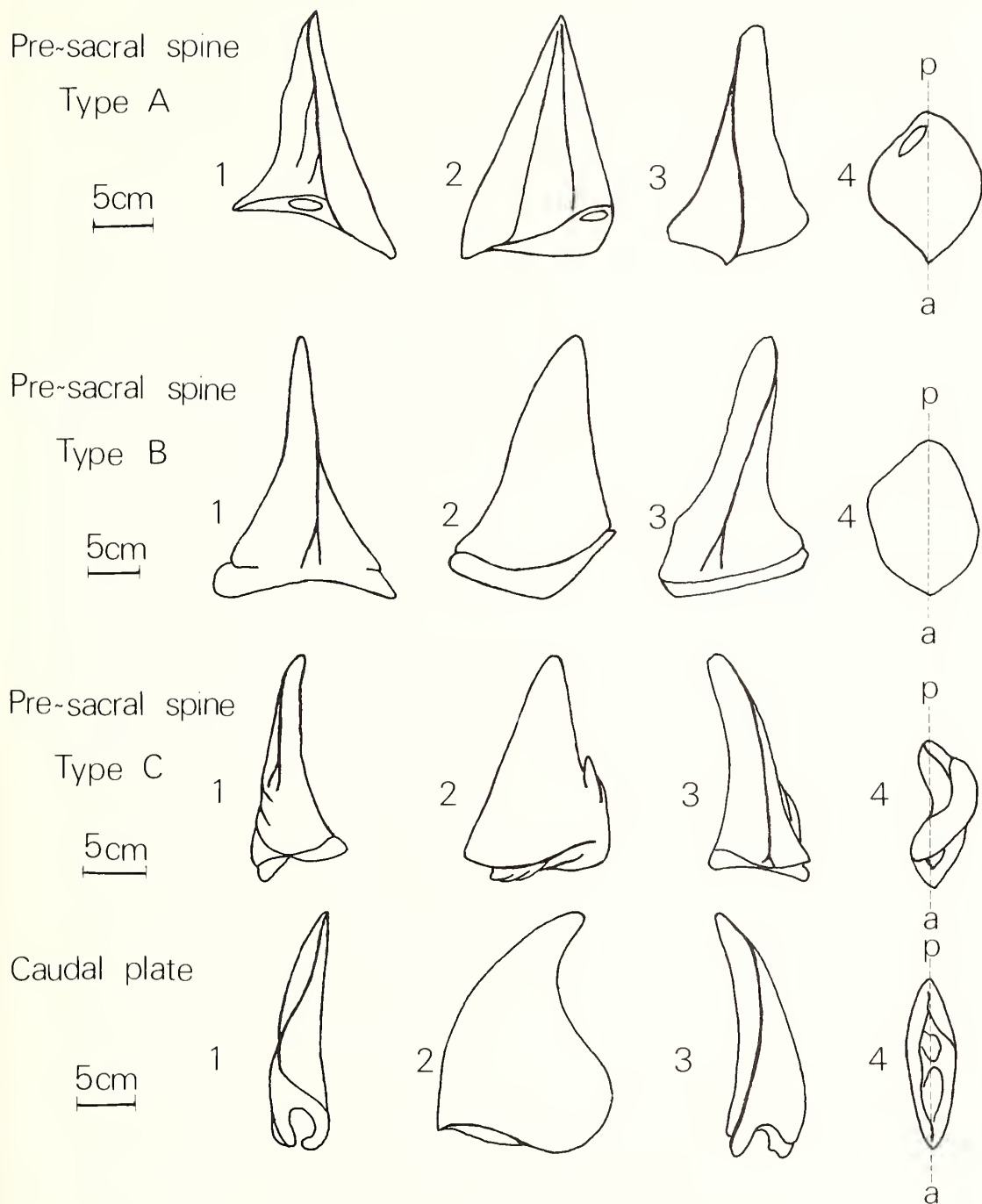
Pelvis. The pelvis is well understood from the holotype (Hulke 1887). Two fragments of ilium found with the new specimen are poorly preserved and offer little new information. An acetabulum with proximal end of the ischium was badly worn before burial. An anterior fragment of ilium shows the dorsal surface not seen in the holotype because of the overlying sacral shield. This surface is generally flat but roughened, especially along the lateral border. A portion of pelvis (BMNH R1926, Beckles Collection) was considered to be a different species of *Polacanthus* (*P. becklesi* Hennig 1924) because of smooth dermal armour and greater thickness of ilium than the holotype (Seeley 1891). It is the medial aspect of the acetabulum with attached eroded sacral ribs and proximal end of ischium, apparently uncrushed but water worn. The fragment of ilium from R9293 is broken but undistorted, and demonstrates varying thicknesses approaching that of the Beckles specimen. Possibly, the holotype may have been subject to earth pressure causing an artificial thinning of the ilia (Lydekker 1891). This is not a factor on which to found a new species (the question of smooth dermal armour will be taken up later).

Seeley (1891) described a bone suggested by him to be the pubis of *Polacanthus* (removed by Nopcsa 1905, to an *Iguanodon*-like genus), the pubis of nodosaurs being much reduced to a ridge on the anterior border of the acetabulum (Coombs 1978).

Limbs. No elements of the limbs have been recovered from the new specimen site except a single terminal phalanx. Hulke (1881) briefly described some bones, considered as 'unguals' by William Fox, as 'broad, depressed and blunt'. The number is not stated, and now I can only define one terminal phalanx among the isolated parts of the holotype. This specimen measures 82 mm long by 63 mm at the widest point, but it is distorted by compression, and this may have caused the articulating surface to appear on the ventral side. The bone has a rounded termination, and no narrow 'neck' between the articulating surface and the body of the phalanx, possibly an adult feature. The terminal phalanx from the site, considered part of the same skeleton, is smaller than the holotype, more pointed and has a flatter base. A slightly narrowed neck gives rise to expanded lateral borders over the anterior two-thirds of the bone. These are separated from the raised body by grooves anteriorly. The neck of the bone is possibly a juvenile feature compared to the holotype unguis, suggesting further the sub-adult status of the new specimen.

Bones of undefined origin. The new specimen includes a small, complete bone of unknown origin. Its appearance is suggestive of a dermal scute, and this was the label attached to its counterpart in Cambridge (SMES B53372). The two are a bilateral pair and originate from the same locality. Each has a sharp-edged ridge across the superior surface with a low peak set at one end. The base inclined to the ridge at an angle of about 45°, and is gently concaved and roughened to suggest a sutural surface with another bone. The shape of the base is oval, but broader at one end than the other. The surface features are unlike other dermal elements, and the existence of an exact bilateral pair is suggestive of possible endoskeletal origin. However, microscopic examination of the surface is suggestive of dermal origin (D. Cooper, pers. comm.). The two do not in themselves unite, but appear to form mirror images some distance apart. Until more complete material is available the origin, orientation, and symmetrical designation of these bones will be in doubt.

Armour. The dermal elements of *Polacanthus* were interpreted by Nopcsa (1905) for the holotype, and the new specimen falls broadly within this scheme. The animal had a bilateral row of dorsolateral



TEXT-FIG. 5. *Polacanthus foxi*. Lower Cretaceous, Isle of Wight. BMNH R9293, presacral and caudal spines. 1, posterior view; 2, medial view; 3, anterior view; 4, inferior (basal) view, a—anterior, p—posterior.

spines of varying height and broad bases along the neck and thorax. The caudal region had a double row of narrow plates set dorsolaterally in decreasing size from tail root to tip. The pelvis and sacrum are covered by a large sacral shield, and numerous smaller ossicles were distributed across the trunk and tail between the larger elements. This arrangement is well understood from description of the holotype, but each of the components are worthy of reassessment in the light of the new specimen. In addition, new dermal elements, unknown in the holotype (Blows 1982), are described.

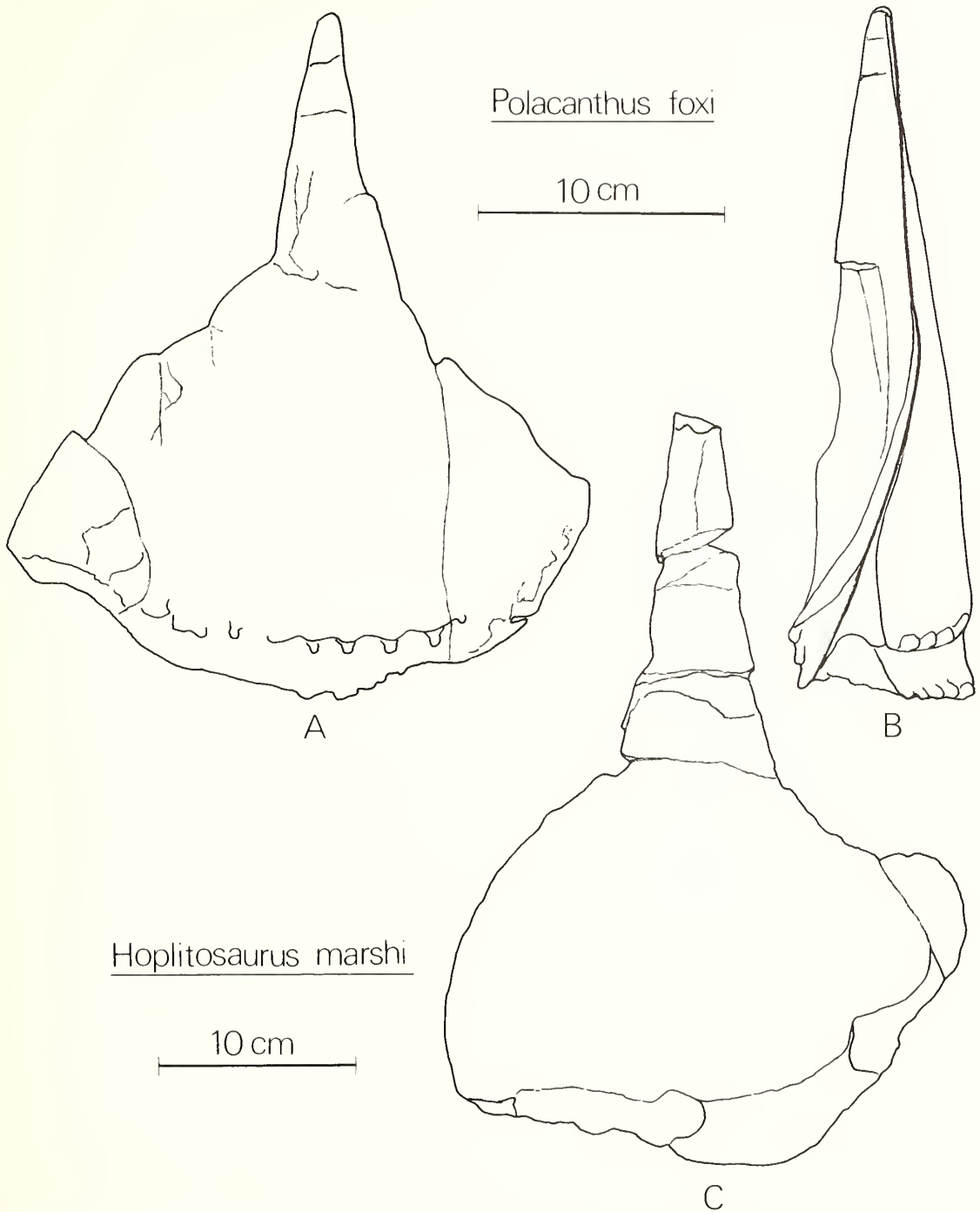
Presacral dorsal spines. The holotype has seven preserved spines (Type A, text-fig. 5), five more are plaster replicas for display purposes. Nopcsa quotes eight spines and distributes them as three left and five right. His illustration (Nopcsa 1905, pl. xii) of the skeleton indicates seven spines as preserved, five right and two left. The new specimen has four recognizable spines (Type A) of various sizes.

Each Type A spine has two distinct edges to the keel which unite at a sharp summit. In the largest spine (text-fig. 8) the two keel edges twist through nearly 90° towards the summit. The bases are solid, broad, flat, and generally asymmetrical; only the smallest spine showing some degree of concavity and symmetry in the base. The base has a hook-like feature produced by an extension of one keel edge below the base margin. Opposite this the larger spines have a groove just inside the base margin. Following Nopcsa in the orientation of the larger spines, the lateral face of the keel is smooth and slightly concave, the medial face is angled into three planes. All the faces of the keel are irregularly grooved, often thought to be of vascular origin, and the base has a crossing fibrous texture.

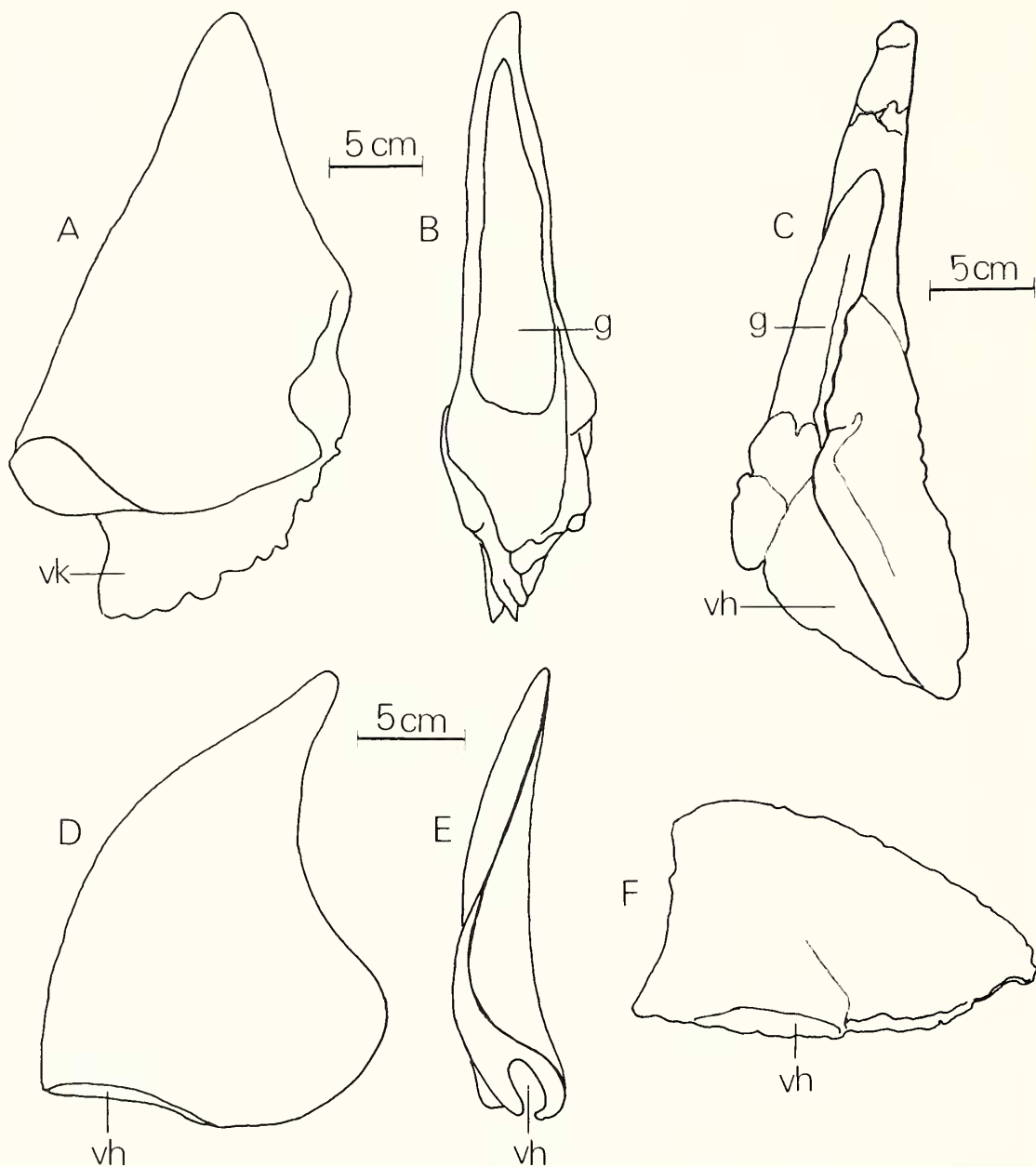
Several of these spines of the holotype are unusually flat and broad, possibly further evidence of general post-mortem crushing. Nopcsa's orientation of these spines shows a consistent pattern. The anterior keel edge is curved outwards, the posterior edge being shorter. This makes the basal hook-like feature anterior, the opposite groove in larger spines being posterior. Other spines are of a slightly different nature (Type B, text-fig. 5). They are MIWG 1191a, a large dorsal spine missing the top, from Sedmore Point, Isle of Wight; and MIWG 5307, a large complete dorsal spine from grey marls several hundred metres east of Chilton Chine, Isle of Wight, about 11 ft. above beach level. They are both presacral in origin because they have solid, broad bases, but they vary from Type A by the following points: the dorsal keel is flat on both sides and the edges are straight, or very gently curved, twisting slightly or not at all. The base has two distinct areas of dermal attachment, a prominent medial anterior process and lateral posterior process. Both areas are separated from the dorsal keel by a step in the bone. There is no hook-like feature in Type B spines. These spines could reach the size of Type A (see MIWG 1191a). Two spines from the new specimen are of the same general variety as Type B, one larger and one smaller, but differ by having narrower, smooth and gently arched bases. These do not reach the full extent of the dorsal keel edges which extend beyond the anterior limit of the base into a V-shape similar to caudal plates. Type C is designated to these spines.

Postsacral caudal plates. The other free standing elements are tail plates extending along the tail in descending size and shape (text-figs. 5 and 7). The holotype has fifteen tail plates set in two rows, seven right and eight left. Nopcsa's skeletal restoration illustrates twenty-two caudal plates in eleven pairs (including the tail tip plates as a pair). The new specimen has five plates referable to the tail, with a number of fragments of others. Three plates are left side and two right, with four fragments referable to the right. The dorsal keel is flat on both sides and tapers to a round peak. The base is narrow and hollowed throughout the posterior two-thirds, the cavity created extending as much as 40 mm into the plate. The base edges are asymmetrical and sinusoidal and are heavily roughened with notches and grooves for dermal attachment. The caudal plates of the holotype differ considerably, the above base shape appears in only one anterior plate (numbered BR1). The others have symmetrical bases with a V-shaped cavity throughout the base length, and a similar hook-like feature to that of Type A spines.

Two caudal plates show variation from this. The first is part of the new specimen (R9293;



TEXT-FIG. 6. *Polacanthus foxi*. Lower Cretaceous, Isle of Wight. BMNH R9293, ?anterior caudal dermal plate, A, ?medial view, B, lateral view. C, *Hoplitosaurus marshi*. Lower Cretaceous, USA. USNM 4752, ?medial view (redrawn from Gilmore 1914).



TEXT-FIG. 7. *Polacanthus foxi*. Lower Cretaceous, Isle of Wight. A, B, GM 981.45, dermal plate; A, ?medial view, B, posterior view. C, *Hoplitosaurus marshi*. Lower Cretaceous, USA. USNM 4752, dermal plate, posterior view (redrawn from Gilmore 1914). D-F, *P. foxi*. Lower Cretaceous, Isle of Wight. D, E, BMNH R9293, caudal plate; D, ?medial view, E, posterior view. F, BMNH R175, caudal plate, ?medial view, g—groove, vh—ventral hollow, vk—ventral keel.

text-figs. 6 and 8) and is distinguished by a long, solid base, the keel narrowing sharply to a peak supporting a straight, narrow cylindrical spine. This spine is nearly half the overall height of the plate, and is similar to the peaks of Type A spines. The length and asymmetry of the plate base suggests early caudal positioning on the left side, possibly the first postsacral plate. The second plate of unusual nature was described previously (Delair 1982) (GM 981.45; text-fig. 7) and is from the Barnes High area of the Isle of Wight (Kemp Collection, 1974). The anterior and posterior edges are straight and the peak is posteriorly inclined. The dorsal keel thickens from the anterior edge to create two posterior edges separated by a groove from base to apex. The solid base supports a rugosed, deep ventral keel for dermal attachment. These plates are discussed later.

Sacral shield. The dermal plate which covered the sacrum and ilium is well known and described by Hulke (1887). This holotype shield is slightly flattened by crushing. It is a complete unit, averaging 8 mm thick, and is not fused to the underlying bone. The dorsal surface is patterned with round, subtriangular or oval bosses bearing various degrees of raised peaks, separated by multiple tubercles and covered with fine grooves. The ventral surface, nor seen in the holotype, has a surface pattern of cross fibrous tissue, like coarse textile (e.g. sackcloth), and is pock-marked by multiple blood vessel openings. Ten large fragments and many smaller pieces exist of this shield in the new specimen (text-fig. 9). The central pieces are thicker, the shield thins towards the lateral and posterior borders. The portion of *Polacanthus* ilium, referred to under 'pelvis' as *P. becklesi* (R1926) was thought to have a fragment of smooth sacral shield attached; this diagnostic feature suggested the new species (Hennig 1924). Close examination of the surface of the armour reveals the bases of at least three bosses and surrounding tubercles; the armour was patterned. This specimen is referred to *P. foxi*, the name *P. becklesi* is obsolete. The holotype shows a very shallow, almost flat patterning to the armour over the same region of ilium as R1926, and the Beckles specimen is clearly badly water worn, being impregnated with calcareous deposits from the sea.

Ossicles. The isolated elements of armour, which were not incorporated within the shield, and which probably covered the dorsum, flanks and tail between the free standing armour were ossicles. They range in size from 9 mm to 70 mm across and number thirty-six from the new skeleton. The larger are subtriangular to nearly round and peaked to one edge, with flat or slightly convex bases. The dorsal surface has vascular grooving. The smaller ossicles are rounded with flat bases. Two ossicles are notched, they have a small rounded piece of one border missing; an incomplete border development and not a fracture. In Sedgwick Museum, Cambridge, about thirteen ossicles exist, all from the Isle of Wight and possibly from this new skeleton. In Sandown Museum, Isle of Wight, a group of dermal pieces (MIWG 37) from Brook contains ossicles of larger size than the maximum collected with the new specimen. One ossicle measures 93 mm by 75 mm, another 60 mm by 100 mm. The British Museum (Natural History), London, has six ossicles plus thirty-nine of the holotype (twenty-eight small, eleven large). Some of the holotype ossicles are the largest known for this genus (e.g. 105 mm by 93 mm).

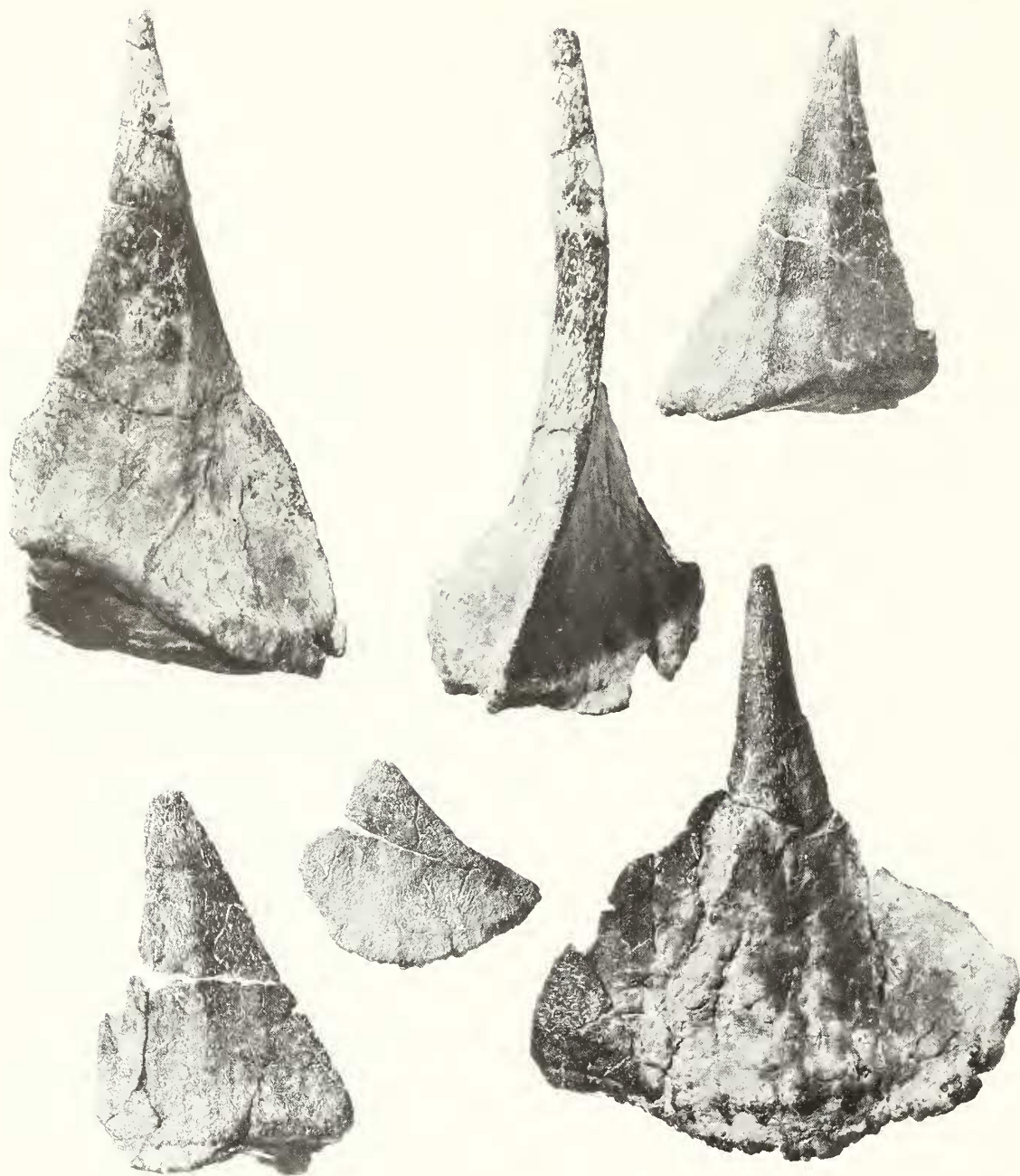
Summary of dermal armour in *Polacanthus* (text-fig. 10):

1. Presacral spines; Type A (both holotype and R9293), a bilateral row; Type B (isolated specimens, MIWG), a bilateral row(?); Type C (R9293), a bilateral fringe (?).
2. Sacral shield (both holotype and R9293) covering pelvis and sacrum.
3. Caudal plates; roof-like (holotype) or tall (R9293) both descending in size in a bilateral row down the tail; Hoplitosaur-like (R9293) (?) anterior plate only.
4. Ossicles; subtriangular or round between other elements (both specimens).

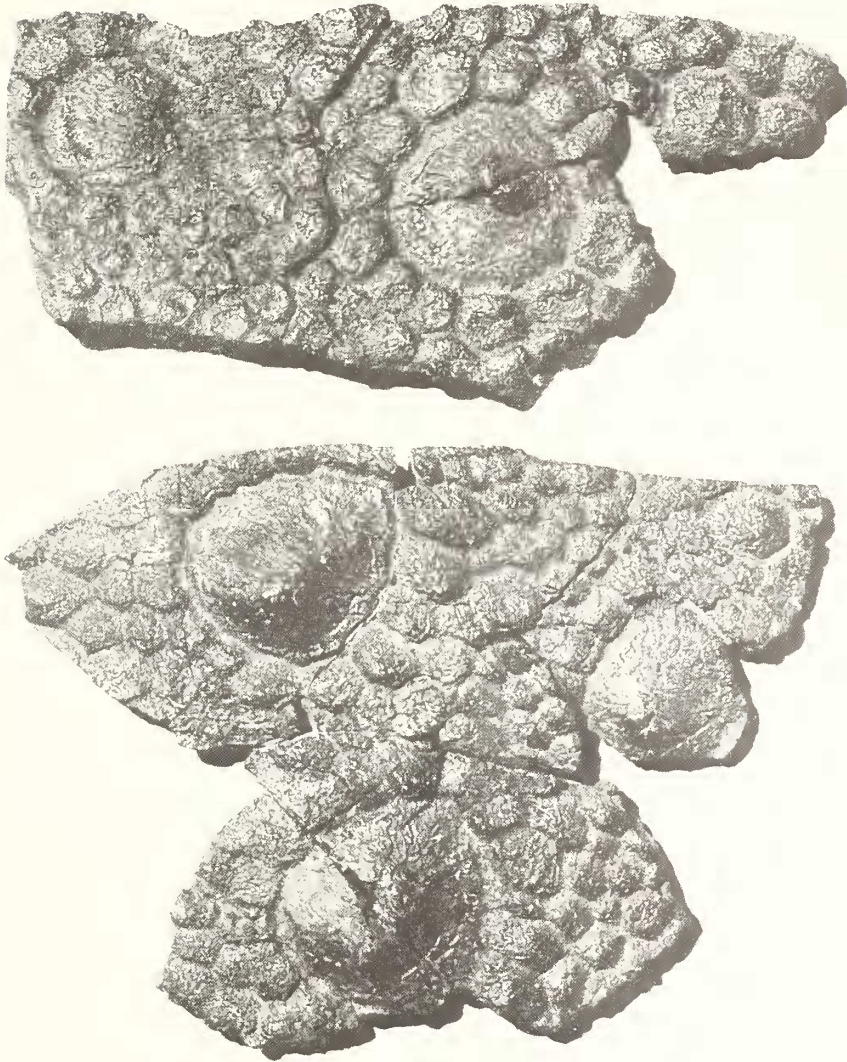
DISCUSSION

Preservation

The new specimen is considerably less complete and more disarticulated than the holotype, yet better preserved. The holotype is distorted by crushing throughout various sections, but crushing in the new specimen is limited.



TEXT-FIG. 8. *Polacanthus foxi*. Lower Cretaceous, Isle of Wight. BMNH R9293, dermal spines and plates. Top row: Type A presacral spines. Bottom row: Type C presacral spine, posterior spine and *Hoplitosaurus*-like caudal plate.



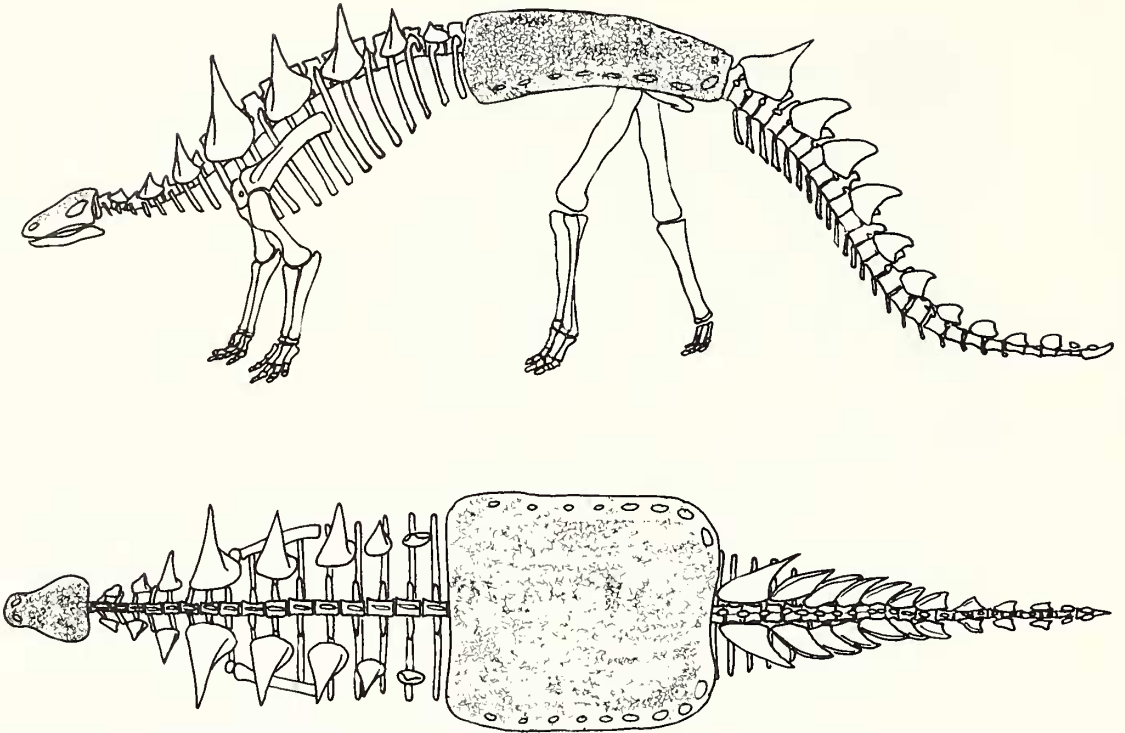
TEXT-FIG. 9. *Polacanthus foxi*. Lower Cretaceous, Isle of Wight. BMNH R9293, dermal armour, two sacral shield fragments, superior (dorsal) view.

Age

The sub-adult status of the new specimen is indicated by separated sutures within the skull fragments, the elements of the atlas vertebra are separated and the characteristic shape of the terminal phalanx.

Post-cranial skeleton

The skeleton of *Polacanthus* is very similar to *Stegosaurus* in many detailed and overall structures, suggesting a possible parallel evolution from a single source; the nodosaurs expanded more rapidly after the decline of the stegosaurs. The osteology of stegosaurs is now well known (Gilmore 1914; Ostrom and McIntosh 1966).



TEXT-FIG. 10. *Polacanthus foxi*. Lower Cretaceous, Isle of Wight. Restoration of skeleton, lateral and superior views. Based on BMNH R175 and R9293.

Post-cranial armour

The structure of Lower Cretaceous nodosaur dermal anatomy is always difficult because the material is usually isolated or disarticulated from endoskeletal remains. Nopcsa's interpretation (1905) of the arrangement of presacral spines remains valid. The angle between the spine base and dorsal keel suggests a position on the animal approximately 40° from the mid-line; a dorsolateral position. The presence of Type C spines in association with the new specimen possibly suggests a lateral fringe over the shoulder region (as in *Palaeoscincus* Matthew 1922) or perhaps a similar arrangement at the tail base. The lateral position of these spines is suggested by the unusual base shape and deep dermal insertions; the weight of the spine would not be directly above the body, creating a need to withstand gravitational forces.

The existence of Type B spines as purely isolated elements causes problems. They strongly suggest a similar position as Type A spines, but their absence in skeletons remains unexplained. No Type B spine can therefore be directly attributed to *Polacanthus* on the basis of known material. However, with absence of other nodosaurs identified from the Isle of Wight Wealden strata, tentative assignation of Type B spines to *Polacanthus* is made on the grounds of possible sexual diamorphism. The discovery of Type B spines in association with other skeletal material will resolve this.

Variation within the caudal plates occurs between the holotype and the new specimen. In the former, only the most anterior plate is of the type described in the new specimen, the others create diminishing roof-like structures along the tail, and flat rounded elements at the tail end. The most anterior plate of the new specimen is probably the Hoplitosaur-like plate with the central spine, unlike any other seen in the holotype. The significance of these two tail armours may be sexual or suggestive of species variation. If sexual diamorphism could be demonstrated in dermal structures,

the caudal plate variation and robust (R9293) or slender (R175) presacral spines could be suspected as such in *Polacanthus*.

The Hoplitosaur-like plate may be indicative of closer affinities with the American Lakota genus *Hoplitosaurus* (USNM 4752). The caudal plate described by Delair (1982) (GM 981.45) enhances the *Polacanthus*-*Hoplitosaurus* link. The assignment of this specimen to *Polacanthus* is tentative on the grounds that a wider range of armour existed within this genus than previously known, and there is no evidence of another genus within the Lower Cretaceous of the Isle of Wight. The structure of the plate is similar to those of an early caudal position and the deep ventral keel is indicative of a lateral projection where deep dermal insertion is needed to overcome gravitational forces.

Histological examination of *Polacanthus* dermal armour has been carried out by Dr Cooper of Worthing. He sectioned both small presacral spines and sacral shield. He writes 'They show the same features of ossified collagen bundles which pass at random in all directions. This armour has clearly formed by transformation of dermal collagen directly into bone, i.e. by metaplasia of collagen as in a tendinous insertion into a long bone. There has then been subsequent formation of marrow spaces and a few Haversian systems in the armour. There is no evidence that any of the dermal elements formed from cartilage or had any form of muscle attachments. The fine channels on the surface of the armour could well be vascular but could also be to increase the surface area of the bone-keratin interface to provide a very rigid attachment for the keratin horn' (D. Cooper, pers. comm.).

The accepted function of dermal elements has always been their protective value against predators. Recently, some work has been conducted on heat dispersal properties of dermal plates in *Stegosaurus* which is well endowed with these elements (Farlow *et al.* 1976).

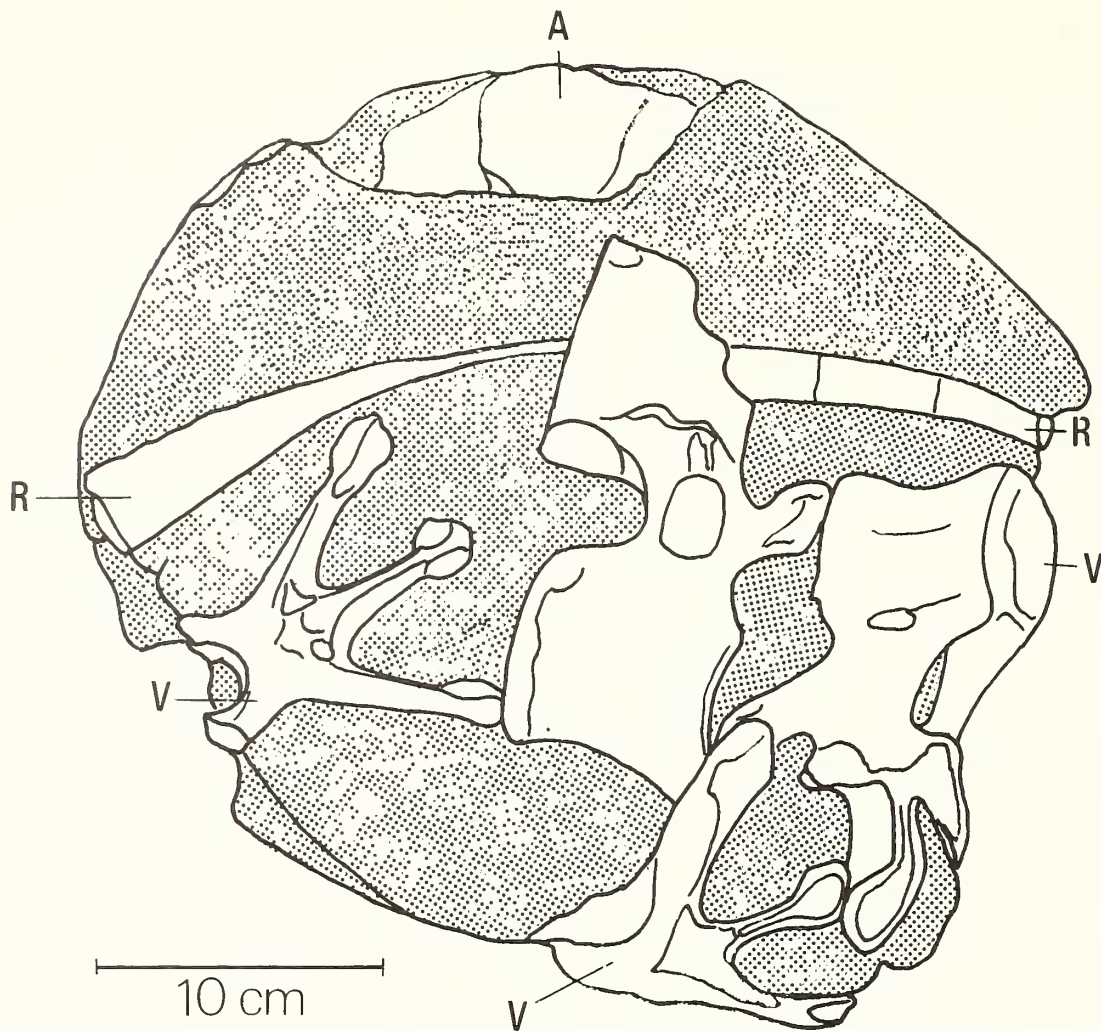
Dr Cooper writes 'I do not think now that one can compare *Polacanthus* armour with the plates of *Stegosaurus* which appear to have a heat radiating function, though similar heat exchange might incidentally occur in the larger lateral spines. However, their primary function is obviously armour protection' (D. Cooper, pers. comm.). A dual purpose may seem incompatible. Should such elements become damaged in a predator confrontation a high vascularity necessary for heat dispersal could predispose to severe blood loss. Selective and well-controlled vasoconstriction would be essential, as postulated for *Stegosaurus* (Farlow *et al.* 1976).

THE RELATIONSHIPS OF *POLACANTHUS*

1. *Polacanthus* with *Hylaeosaurus*

Coombs (1971) and others suggest that *Polacanthus* and *Hylaeosaurus* are possibly synonymous. *Hylaeosaurus* appears limited to the South East English mainland geology, which occupies most of the Wealden Series from Ryazanian to Barremian (Rawson *et al.* 1978). *Hylaeosaurus* has occurred in the 'Tilgate Forest' (Mantell 1841; Owen 1856) which probably refers to the Tilgate Stone (Gallois 1965), extensively quarried in Mantell's day, and the strata from which he obtained *Iguanodon*. It is also known as Cuckfield Stone (Rawson *et al.* 1978), and divides the Grinstead Clay into Upper and Lower components (Hastings Beds). The palaeontological record is grossly incomplete, but the current evidence restricts *Hylaeosaurus* to the Upper Valanginian (Tunbridge Wells Sand/Grinstead Clay), which is unexposed on the Isle of Wight.

Polacanthus ranges from Wealden Marls to (?) Ferruginous Sands (Barremian to Lower Aptian) mostly from the Isle of Wight with one specimen from the mainland. This is a slab of grey matrix from the Greensands overlying the Lias at Charmouth, Dorset, and containing parts of four disarticulated but associated dorsal vertebrae, a rib section, and portions of flat dermal armour (sacral shield) (text-fig. 11). Between the ranges of the two genera a gap occurs in the Lower Weald Clay (Hauterivian). This may well be a collecting anomaly, or may have evolutionary significance. Currently it suggests a geological separation between the two genera, with *Hylaeosaurus* being considerably the older. The *Polacanthus* range correlation on the mainland (Upper Weald Clay to



TEXT-FIG. 11. *Polacanthus foxi*. Middle Cretaceous, Charmouth, Dorset. Dorsal vertebrae, rib and sacral shield armour in matrix.

Hythe Beds) does not seem to yield this genus. It is important to realize that the rarity of nodosaurids and the inadequacy of Wealden collecting (especially of the mainland) constitutes a vestige of material from which positive conclusions are difficult.

In *Hylaeosaurus* the series of long pointed spines appear to take a lateral fringe position over the shoulder region, similar to the arrangement in *Palaeoscincus* (Matthew 1922; Gilmore 1930). Post-mortem displacement is limited, as indicated by the largely articulated nature of the endoskeleton. The presacral spines of *Polacanthus* appear to be positioned more dorsolateral, and Types A or B are not found in the holotype or referred specimens of *Hylaeosaurus*. The shield of armour in *Polacanthus* is found as fragments on the Isle of Wight. No evidence exists of this shield in *Hylaeosaurus*, and no fragments of sacral shield are known from the mainland Wealden formation or referred to *Hylaeosaurus*. A similar situation occurs with ossicles, which are numerous, variable in shape, both large and small in *Polacanthus*, but remain rare in *Hylaeosaurus*, being round, small

and button-like. Caudal plates also are scarce in *Hylaeosaurus*, a nearly complete tail (BMNH 3789) has the bases only preserved of what could be two caudal plates, whilst both *Polacanthus* discoveries are dominated with caudal armour. The current evidence suggests that *Hylaeosaurus* was a primitive nodosaurid existing earlier than *Polacanthus*, and having a different armour arrangement. At present, these two genera should be considered completely separate.

2. *Polacanthus* with *Polacanthoides*

Nopcsa's (1928) *Polacanthoides* can be dismissed on the grounds that:

a, two bones (BMNH R1106 and R1107) are from the Isle of Wight and not from 'Bolney, Sussex' as stated by Nopcsa (1928); *b*, they are casts, the originals returned to the Isle of Wight and are now lost, and therefore should not have been designated as holotypes; *c*, the scapula (BMNH 2584) from Bolney, Sussex is clearly associated with a tibia (BMNH 2615) (Mantell 1841, p. 143; Lydekker 1888), but Nopcsa (1928) does not mention this tibia.

The difference between the scapula of *Hylaeosaurus* and *Polacanthoides* is the acromion process; large and flange-like in *Polacanthoides*, thumb-like in *Hylaeosaurus* (Nopcsa 1928; Ostrom 1970). Ostrom upheld the distinction of *Polacanthoides* from *Hylaeosaurus*, but Coombs (1978) synonymizes the two genera, and finds the acromion size to be no grounds for the foundation of a genus. The name *Polacanthoides* (and thus *P. ponderosus*) is *nomen dubium*. The tibia and humerus (BMNH R1106, R1107) (Hulke 1874) are from the Isle of Wight, and may be *Polacanthus*. The tibia is very similar to *Polacanthus* (Ostrom 1970, p. 135), but no humerus is known of *Polacanthus* for comparison. On geological grounds these two bones may be referable to *Polacanthus* rather than *Hylaeosaurus*.

3. *Polacanthus* with *Hoplitosaurus*

The new *Polacanthus* has suggested close affinities with the American genus *Hoplitosaurus marshi* (Lucas 1902; USNM 4752). Both genera have flat and standing dermal elements. *Hoplitosaurus* armour is described by Gilmore (1914, pp. 118–121), and I refer to his numbering:

- 1, simple flattened, which correspond to variations within the ossicles of *Polacanthus*;
- 2, rounded ossicle-like, which correspond to ossicles of *Polacanthus*;
- 3, keeled, which correspond to ossicle variation within *Polacanthus*;
- 4, triangular, plate-like, which correspond to caudal plates of *Polacanthus*, in particular R9293;
- 5, spined, of which he recognizes the following sub-types:

a, 'scutes', which correspond with the *Hoplitosaurus*-like plate of R9293 (Gilmore 1914, pl. 28). Gilmore misinterpreted Nopcsa (1905) by thinking such elements were placed anterior to the sacral shield. In fact, no elements of this kind exist in the holotype (R175), the first European plate of this type occurs in R9293. Some presacral spines of R175 have a similar central spine, but differ in having broader, plain bases. It is easy to see how this plate type has developed from the presacral spines but has caudal plate qualities. The position is therefore most likely to be the first plate, immediately behind the sacral shield. It would seem that R175 never did possess such a plate, whilst R9293 and USNM 4752 did. Whether this is an indication of sexual variation, along with the difference in caudal plates between R175 and R9293, is unknown.

b, dermal elements with grooved posterior borders, of which only one English example exists, GM 981.45 from the Weald of the Isle of Wight (Delair 1982). The presence of grooved plates in *Hoplitosaurus* (Gilmore 1914) suggests the possible inclusion of the English plate within the genus *Polacanthus*. The deep ventral keel is its only unique character, suggestive of deep dermal insertion to overcome gravity.

c, compressed spines with heavy, massive, expanded bases, comparable to the presacral (Type A) spines of *Polacanthus*.

Hoplitosaurus and *Polacanthus* dermal armour compares well. The absence of a sacral shield in *Hoplitosaurus* may be the only objection, although reference is made to this under (2) above (in Gilmore 1914, p. 118). The two could be found synonymous, in which case *Polacanthus* (Huxley

1867) takes priority over *Hoplitosaurus* (Lucas 1902). If the sacral shield was considered sufficient grounds to allow species differentiation then *Polacanthus marshi*, new combination, could be reserved for USNM 4752. This synonymy would extend the geographical range of *Polacanthus* outside England to the American Lakota Formation as suggested for other Isle of Wight genera, e.g. *Hypsilophodon wielandi* (Galton and Jensen 1979).

CONCLUSIONS

Polacanthoides ponderosus is not valid. *Polacanthus* and *Hylaeosaurus* are separate genera. *Hoplitosaurus* is probably a subjective junior synonym of *Polacanthus*, possibly extending the range of *Polacanthus* into America. If species differentiation was shown between the two holotypes, *P. marshi*, new combination is proposed for USNM 4752.

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APPENDIX I

Specimens of Polacanthus foxi Hulke 1881

Holotype: BMNH R175, partial skeleton; Referred specimens: MIWG 37, seven ossicles, one tail plate base; MIWG 4222, one ossicle (Poole Collection); MIWG 1983, one ossicle, one sacral shield fragment; MIWG 5144, caudal vertebra; MIWG 5307, dorsal spine (collected April 1983); MIWG 5145, caudal plate fragment; MIWG 5186, six plate fragments, one ossicle; MIWG 5187, two ossicles; MIWG 1191a, dorsal spine; MIWG 5188, dorsal centrum; CAMSM B53595, dermal ossicle; CAMSM B53594, small dermal ossicle; CAMSM B53590, dermal ossicle; CAMSM B53588, dermal ossicle; CAMSM B53589, dermal ossicle; CAMSM B53591, dermal ossicle; CAMSM 53597, dermal ossicle; CAMSM B53371, axis vertebra; CAMSM B53372, unidentified bone; CAMSM B53353, large dermal ossicle; CAMSM B53354, flat ossicle; CAMSM B53358, flat ossicle, CAMSM B53357, ossicle; CAMSM B53355, ossicle; CAMSM B53356, ossicle; CAMSM B53596, dermal ossicle; CAMSM B53587, dorsal vertebra; CAMSM B53593, dermal ossicle; BMNH R4952, caudal vertebra (Gunyon Collection 1923); BMNH 36515-36517, two dermal spines (Mantell Collection); BMNH 40458, dermal ossicle; BMNH 37713-37714, two dermal ossicles (Saul Collection 1863); BMNH R643, dermal ossicle (Lee Collection 1885); BMNH R1876, dermal plate (Beckles Collection); BMNH 34533, dermal ossicle (Backhouse Collection); BMNH R1875, dermal spine (Beckles Collection); BMNH R2527, dorsal vertebra (Hulke Collection 1869); BMNH 39556, rib head; BMNH R202, two ossicles; BMNH R202-R202(A), four dermal spines (Fox Collection); BMNH R203, two dermal spines (Fox Collection); BMNH R1926, ilium fragment with sacral armour (type of *P. becklesi*) (Beckles Collection); BMNH R4134, vertebral process and rib head; BMNH R9905, sacrum; BMNH R9293, partial skeleton with dermal armour (Blows Collection 1979) and cervical vertebra; GM 981.45, dermal plate (Kemp Collection); block containing dorsal vertebrae, rib, and dermal armour (private collection); spine and caudal vertebra (Ford Collection).

APPENDIX II

Table of measurements in millimetres:

i. Cervical vertebrae

	SMES B53371	BMNH R9293
Length of centrum	54	50
Width of anterior surface	64	65
Height of anterior surface	40	43
Total height of vertebra	80	107
Greatest width of neural canal	25	23
Greatest height of neural canal	25	30

ii. Dorsal vertebrae

		Length of centrum	Height of centrum	Width of centrum		Height of neural canal		Overall height
				Anterior	Posterior	Anterior	Posterior	
Holotype	C12	62	50	—	61	30	25	130+
R175	C14	77	51	53	52	23	25	110+
	C16	—	—	—	—	—	—	—
	C18	—	—	—	58	—	48	—
	C19	80	50	56	52	—	—	—
BMNH R9293	1	70	53	61	61	25	30	—
	2	—	56	63	—	25	—	130+
	3	75	59	63	56+	22	27	150+
	4	73	57	63	65	22	31	135+
BMNH 2527		84	73	82	—	23	—	212+
SMES B53587		78	60	68	69	23	24	144+
MIWG 5188		70	60	71	70	—	—	—
Charmouth specimen		70	65	—	—	—	—	170

iii. Sacral vertebrae

	R175	R9293	BMNH R9905
Length of five sacral centra	350	365	360
Length of five presacral centra	410	—	—
Width of posterior articular surface (S5)	—	78	—
Height of posterior articular surface (S5)	—	50	—
Maximum width of neural canal (S2-S3 level)	—	78	—
Maximum height of neural canal (S2-S3 level)	—	60	—
Maximum width between (R) and (L) sacro-iliac joints	418	—	425

iv. Caudal vertebrae

	R175		R9293		R9252	MIWG 5144
	1st	2nd	1st	2nd		
Overall height	—	165	146	155	107+	—
Length of centrum	60	50	60	55	40	45
Width of centrum	85	90	83	82	52	55
Height of centrum	40	60	58	60	52	60

v. Terminal phalanges

	R175	R9293
Total length	82	60+
Greatest width	60	35
Height of articular surface	20	19
Width of articular surface	50	29

vi. Measurements of spines (Type A)

	Total height	Length of base	Width of base
Holotype, BMNH R127			
R2 (f6), large spine	325+	205	100
R4 (f4)	305+	230	90
L1 (g7), medium spine	322	198	115
L2 (g6), large spine	392+	210	110
R3 (f5)	340+	215	111
R5 (f3), medium spine	175+	190	110
R4 (f1), smallest spine	90	140	80
BMNH R9293			
Largest spine, left side, shoulder	322 approx.	190	148
Large spine base, left side	—	197	95
Medium spine, right side	215 approx.	140	95
Smallest spine, anterior to pelvis	90	117	74

vii. Measurements of spines (Type B)

	MIWG 1191a	MIWG 5307
Overall height	—	260
Length of base (along keel)	—	170
Width of base (opposite keel)	—	130

viii. Measurements of spines (Type C)

	BMNH R9293	
Overall height	207+	195+
Length of base (along keel)	200	120
Width of base (opposite keel)	130	50

ix. Measurements of plates

	Overall height	Length of base	Greatest width of base
Holotype, R175			
Early caudal, BR1	200+	—	—
Middle caudal, BL3	110	192	—
Late caudal, BR6	70	126	—
BMNH R9293			
Spined plate, left	280	238	58
Early caudal, left	245+	218	42
Early caudal, left	230	—	45
Early caudal, left	210	160	40
Early caudal, right	200+	200	45
Late caudal, right			
GM 981.45			
Early caudal(?)	330	160	60

x. Measurements of modified ossicles

	SMES	MIWG
Maximum width across base	87	77
Length of base parallel to keel	70	67
Height of ossicle	38	37

xi. Bilateral bones of unknown origin

	B53372	R9293
Length (overall)	40	39
Height (overall)	30	29
Length of base	35	34
Width of base	20	20